Simulation of nitrogen rhizodeposition and assimilation back into corn (*Zea mays* L.) roots

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Abstract

The objectives were to quantify the dynamics of N exchange between corn root and soil under field conditions and to compute the amount of N-rhizodeposition that is recycled back into corn by maturity. In a previous publication the simulation model NCSWAP/NCSOIL was used to quantify the release of organic-C from corn and its incorporation into soil organic matter. In this publication, results from the same simulations but pertinent to N are presented. The model was calibrated against measured N concentration in corn and soil and ^{15}N enrichment data obtained from a long-term field experiment located near St Paul, MN. Field management included rototillage, the removal of stover-residue and grain and 4 fertilizer N treatments: 200 and 20 Kg N ha^{-1} added yearly from 1980 to 1992, with ^{15}N added with the fertilizer from 1980 until either 1985 or 1992. The same total amount of ^{15}N was added with the 200 and 20 Kg N ha^{-1} fertilizer: 4 and 40 ^{15}N at.%, respectively. Corn roots released 24% of total N uptake. This loss was mitigated by the recycling of 14% of N-rhizodeposition into corn by maturity. ^{15}N enrichment in corn and soil was higher for the 200 than the 20 Kg N ha^{-1} treatment. This resulted from the rapid N mineralization–immobilization turnover that channelled N through the inorganic N pool whose ^{15}N enrichment was fixed yearly to that of the fertilizer. Tracer N enrichment decreased more rapidly in corn than in soil from 1986 to 1992 when tracer N was no longer added with the fertilizer, and by 1992, ^{15}N was localized in the stable pool and flushed from the more labile pools.
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1. Introduction

Rhizodeposition of C from plant roots is well documented. Photosynthates are transferred below ground, leaked as exudates or sloughed off rootlets and decayed in the rhizosphere (Balesdent and Balabane, 1996; Clapp et al., 2000; Molina et al., 2001). Along with C, N is also released, incorporated into the soil organic matter (SOM) and made available to plants as NH_4^+ by the mineralization–immobilization turnover (MIT). For example, up to 57 and 49% of N assimilated by legumes and barley, respectively, were found in the soil after removal of the roots at maturity (Jansen, 1996a). The decay of rhizodepositions from N_2 fixing plants released NH_4^+ which was available to plants growing in association with legumes (Jansen, 1996b). N released from alfalfa and birdsfoot trefoil originated more through root and nodules decay than exudations (Duback and Ruselle, 1994). N exchange was observed between the roots of an alfalfa-bromegrass sward (Walley et al., 1996).

The high C:N ratio of rhizodeposition from non-leguminous plants induces N immobilization: N is captured in the SOM with a net N loss for the plant from which it originated, even if this N is made available later on for subsequent crops (Huggins and Pan, 1993). This model of N dynamics in the rhizosphere assumes that the rate of net N mineralization from SOM is so slow as to preclude significant recycling of N to the source plant before maturity. Recent publications, however, would indicate that such is not the case. Both the amount of N released by roots and its rate of turnover are high. Høgh-Jensen and Schjoerring (2001) showed that N-rhizodeposition from

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ryegrass exceeded the amount of N present in stubble. The recycling of root-derived N back into winter wheat during the growing season was demonstrated by Jimenez et al. (2002). They estimated that up to 54% of the N assimilated by winter wheat was leaked as rhizodeposition, a loss which was, however, mitigated by the existence of a 'N loop between soil and growing plants'.

Carbon and nitrogen dynamics in the soil-root system are linked. In a previous publication (Molina et al., 2001) we used the simulation model NCSWAP/NCSOIL to quantify the release of organic C from corn and its incorporation in the SOM. The model, calibrated against field data from a long-term experiment with continuous corn, simulated the kinetics of corn above-ground production, SOM, soil δ ^{13}C values, and SOM derived from corn. In this publication, results from the same simulations but pertinent to N are presented. Our objectives were to quantify the dynamics of N exchange between corn roots and soil under field conditions and to compute the amount of N-rhizodeposition that is recycled back into corn by maturity.

2. Materials and methods

2.1. Field experiments and measured data

Data were obtained from ^{15}N microplots (1×3 m) located in the center of plots (6×9 m) established adjacent to the nitrogen, tillage, residue management (NTRM) long-term experiment started in 1980 at the University of Minnesota Outreach, Research and Education Park, Rosemount, MN. The ^{15}N microplots were surrounded by a 30 cm metal barrier pushed 20 cm into the soil. Both field experiments are on-going long-term continuous corn studies. The ^{15}N microplot experiment is a factorial of two rates of N application (200 and 20 kg N ha^{-1}), two corn stover-residue managements (stover removed or returned), and two methods of tillage (garden-size rotary tilled or not tilled). Detailed accounts of the ^{15}N microplots are given by Clay et al. (1985, 1989) and Gollany et al. (2004), whereas details of the adjacent NTRM experiment is detailed by Clapp et al. (2000). This publication presents the data obtained from 1980 to 1992 for the following treatments of the ^{15}N microplots: soil tilled; stover-residue plus grain removed; ammonium sulfate fertilizer N surface applied every year in spring at 200 and 20 kg N ha^{-1} with 4 and 40 ^{15}N at.%, respectively, for a total addition of about 8.0 kg ^{15}N ha^{-1}. The ^{15}N at.% of the added fertilizer N was measured every year. In 1985 the ^{15}N microplots were split in two by a metal barrier similar to the one surrounding the plot. One half continued to receive ^{15}N but the other half did not in order to document the relaxation kinetics of ^{15}N disappearance from plant and soil. There were thus 4 N treatments (2 rates of N fertilizer application $\times$ 2 number of years when tagged N fertilizer was added). The soil at the site is a Waukegan silt loam (fine-silty over sandy or

sandy-skeletal, mixed, mesic Typic Hapludoll). Soil depth to gravel is about 100 cm. The climate is continental (average temperatures in January and July are -12 and 22 °C, respectively, with an annual average precipitation of 840 mm). The ^{15}N plots were rototilled in the fall to a depth of 15 cm or less. Soil samples were taken from 0 to 15 and 15 to 30-cm layers, sieved (2 mm), and analyzed for total and tracer N.

Nitrogen from soil and above-ground corn samples was determined using an elemental analyzer interfaced with a stable isotope ratio mass spectrometer (Carlo Erba, model NA1500 and Fisons, model Optima, Middlewich-Cheshire, UK). Specific field management, soil sampling and analytical techniques were detailed in Clapp et al. (2000).

2.2. Simulated data

Simulated N data were computed from the model NCSWAP/NCSOIL (Molina et al., 1983; Hadas and Molina, 1993; Molina et al., 1997). The source code is available at the web site http://www.soils.umn.edu/research/ncswap-ncsoil/. The model simulates C and N—total and tracer—transformations related to soil water, thermal and solute transport in a soil profile. Optimum above-ground plant growth is represented by functions parameterized for mass increase and N% decrease measured for a reference year when N and water stress are minimal. Plant growth is adjusted for water and N stress by reduction factors. Adjustment to the temperature is achieved by linking the actual and reference air temperatures through degree day accumulation. Root and above ground daily mass increase are linked by a time dependent shoot-to-root ratio. Repartition of root mass in soil layers is controlled by the fraction of the daily root mass increase that is added to the top layers of the profile; the repartition is defined based upon physiological stages of the crop. The root mass not included in the top layers is distributed in the subjacent layers; roots grow until the beginning of decay at harvest or maturity; rhizodeposition decays as soon as formed. The amount of rhizodeposition was specified as the ratio of root-C lost as rhizodeposit to root-C increase per day. The ratio was obtained by calibration of simulated against experimental relaxation ^{15}N kinetics.

N and C transformations are simulated by NCSOIL as a subroutine of NCSWAP. SOM in each 5-cm layer in the 100-cm profile is represented by four pools: labile and recalcitrant Pool I, Pool II, and Pool III. Organic debris in each layer is: (1) roots and (2) rhizodeposition from current year; (3) roots and (4) rhizodeposition accumulated from previous years; (5–7) three different above-ground crop residues; and (8–11) four different organic amendments.

Simulated rates of change in tracer N were computed at each time step as the rate of change in total N multiplied by the ratio of tracer to total N. No discrimination between tracer and total N rates of transformation was assumed. Initial tracer N concentrations of the soil pools were set to
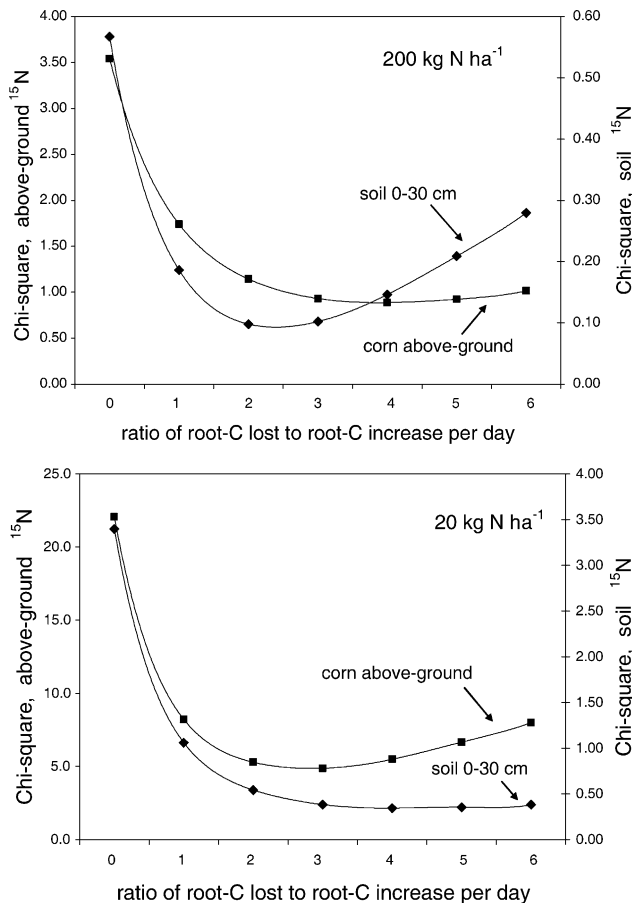
Fig. 1. Sensitivity of ^{15}N excess at.% in above-ground corn and soil (0–30 cm) to variations in the rate of rhizodepositions at 2 fertilizer treatments: 200 and 20 kg N ha^{-1}.

zero. Tracer N enrichments were expressed as excess ^{15}N at.% relative to the measured average natural tracer N concentration of the soil, 0.37675 ^{15}N at.%. Gollany et al. (2004) also give details of the simulation procedure using both ^{15}N and ^{13}C tracer measurements.

The simulated time course of N released from the roots was obtained by tagging N-rhizodeposition. For purposes of this research all pathways of C and N losses from the roots (exudation, passive leakage, tissue decomposition) were treated similarly as rhizodeposition. As N was lost from the root for the first time, the ratio of tracer to total N-rhizodeposition was set to 1.0. For subsequent time steps, the ratio was maintained to 1.0 after accounting for the tracer N recycled through the SOM. This simulation analysis was carried out for the year 1980 with non-tagged 200 kg N ha^{-1} fertilizer. The model assumed that the rapid microbial decay of N-rhizodeposition precluded any direct assimilation of organic N by the roots (Owen and Jones, 2001). The parameters that control C and N transformations in soil—such as half-life of the SOM pools, microbial efficiency of C assimilation and humifi-cation—were assigned the same values as used in previous simulations.

3. Results

3.1. Calibration

The rate of rhizodeposition was obtained for the value corresponding to a minimum of the χ^2-function taken for measured and simulated above-ground and soil (0–30 cm) ^{15}N relaxation kinetics at 200 and 20 kg N ha^{-1} in 1980 (Fig. 1). The χ^2-values dropped sharply from 0 to 2 C released for each C root produced per day and then changed little as the rate increased. Consequently, the daily ratio of the released C to root-produced C was set to 3 for later simulations. A minimum of the χ^2-function could not be obtained for variations in the N% of the rhizodepositions which was set to 0.4 that of the above-ground corn.

3.2. Dry mass and nitrogen

The measured cumulative above-ground dry masses for the high and low N treatments were similar from 1980 to 1983. Subsequently, they gradually diverged (Fig. 2). This trend was reflected in the simulated data. Simulated N concentration in the above-ground corn was diluted from 4.9% at emergence to about 1% at harvest (Fig. 3). The measured N% at harvest was lower for the low N than for
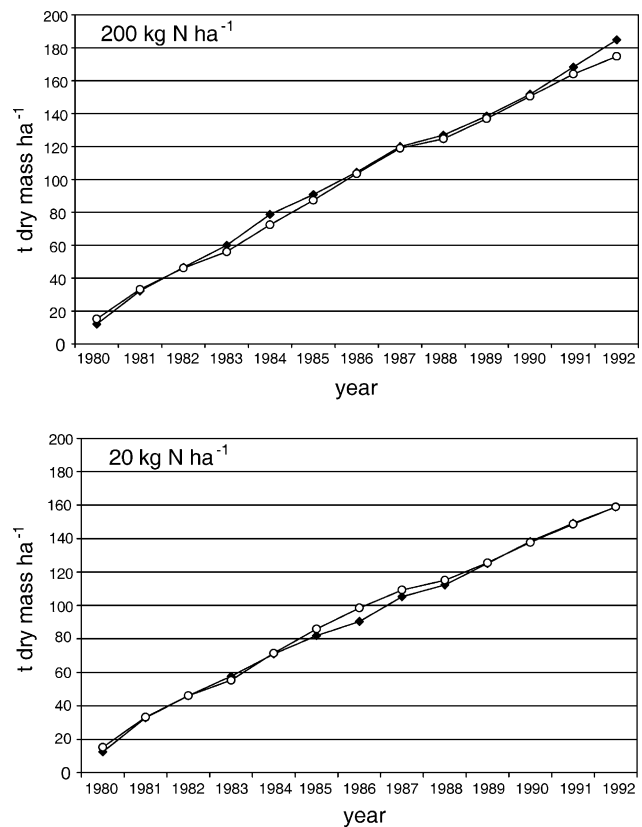

Fig. 2. Cumulative above-ground dry mass for the 200 and 20 kg N ha^{-1} fertilizer treatments: (○) simulated at time corresponding to measured data, (♦) measured.
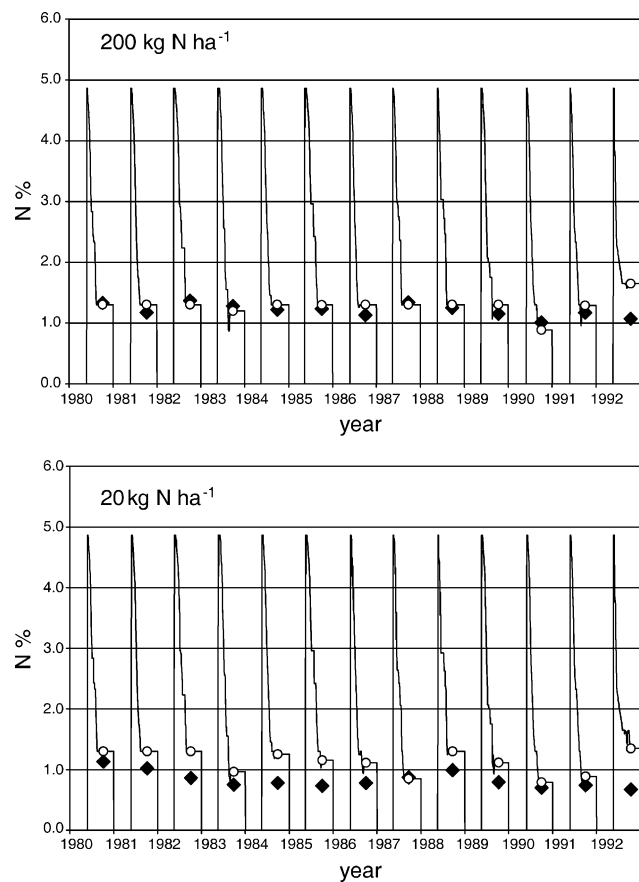
Fig. 3. Above-ground N percentage for the 200 and 20 kg N ha^{-1} fertilizer treatments: (━━━) simulated, (○) simulated at time corresponding to measured data, (◆) measured.

the high N treatment, even for the first 4 years when there was no distinction between the dry mass accumulation at 20 and 200 kg N ha^{-1}. A lower N% with the low N treatment was also simulated but not sufficiently depressed to closely match the measured data (Fig. 3).

The simulated inorganic plus organic N (plant root residues excluded by sieving) decreased gradually at the same rate in the 0–15 and 15–30 cm soil layers (Fig. 4). The addition of 200 kg N ha^{-1} was marked in the top layer by simulated peaks that disappeared with plant N uptake and nitrate leaching. Measured and simulated data were matched in the top layer for both N rates. In the 15–30 cm layer, however, the measured data did not fit the simulated trends and were highly variable in the high N treatment.

3.3. Tracer nitrogen

The measured and simulated dynamics of ^{15}N in the above-ground portion of corn and in soil are shown in Figs. 5–8. Tracer N enrichment in corn and soil both differed with the ^{15}N concentration of the fertilizer N (40 and 4 ^{15}N at.% for the 20 and 200 kg N ha^{-1}, respectively; notice the different excess ^{15}N at.% scales) although the same

amount of tracer N was applied, i.e. 8.0 kg ^{15}N ha^{-1}. ^{15}N enrichment was higher in both corn and soil for the low fertilizer N application.

Every year, a sudden increase in ^{15}N enrichment was simulated in the 0–15 cm soil layer corresponding to the addition of ^{15}N enriched fertilizer N. As inorganic N subsided with corn N uptake and mass transport, this ^{15}N peak stabilized to the ^{15}N enrichment of the SOM. The peaks were less pronounced and occurred with a time lag in the 15–30 cm layer. A better fit between measured and simulated ^{15}N enrichment was obtained in the 15–30 than in the 0–15 cm soil layers; a pattern which is the reverse of that observed with total soil N.

The measured relaxation kinetics exhibited in soil and plant from the microplots that did not receive ^{15}N from 1985 to 1992 was accounted for by the simulation. Tracer N enrichment decreased more rapidly in plant than in soil. Tracer N in soil gradually stabilized at about one-half the level attained in 1985. ^{15}N enrichment in corn decreased suddenly in 1985 to an almost constant low level in subsequent years.

3.4. N exchange between corn and soil

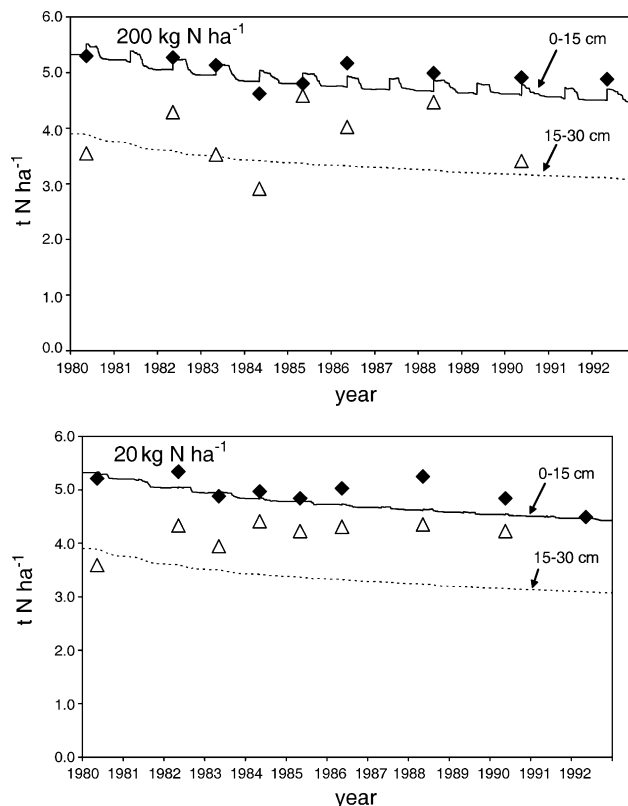The simulated dynamic of rhizodeposition ^{15}N for the year 1980 and in the high N treatment showed that corn

Fig. 4. N concentration in soil for the 200 and 20 kg N ha^{-1} fertilizer treatments: (━━━) simulated, (◆) measured 0–15 cm; (- - -) simulated, (△) measured 15–30 cm.
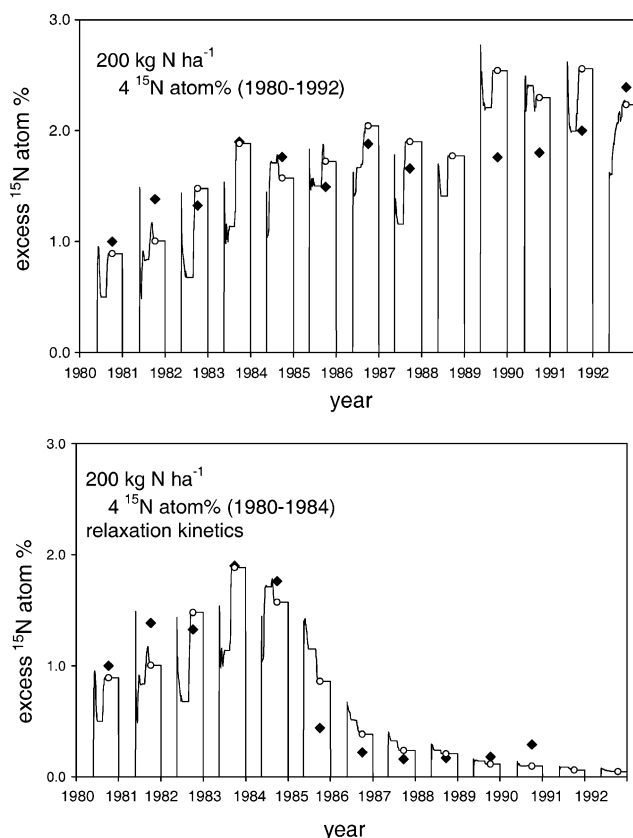
Fig. 5. Tracer ^{15}N in above-ground corn for the 200 kg N ha^{-1} with 4 ^{15}N at.%, and 2 periods of ^{15}N applications: 1980–1992 and 1980–1984: (━━━━) simulated, (○) simulated at time corresponding to measured data, (◆) measured.

roots had leaked 63 kg N ha^{-1} or 24% of the N uptake at maturity (Fig. 9). This was not a total loss for corn because 9 kg N ha^{-1} was reabsorbed by the roots for a net loss of 54 kg N ha^{-1}. Of this net loss, one-half was partitioned at maturity to the SOM, and 30% to inorganic N while 20% remained in the rhizodepositions.

4. Discussion

The level of rhizodeposition was obtained by calibration against ^{15}N enrichment kinetics. The same approach used with the C kinetics gave a wide range of possible values because this parameter had little effect on the simulated kinetics (Molina et al., 2001): most of the information was lost with the unmonitored escape of CO_2. With N, however, the information was kept in the system as losses by denitrification and mass flow were not as extensive as those associated with CO_2.

The trend of measured kinetics for total and tracer N enrichment in corn and the two soil layers was reproduced by the simulation. The ^{15}N concentration effect and the relaxation curves were accounted for by the model. The simulated kinetics resulted from several processes that run simultaneously, competed for N and were quantitatively

integrated by the model. Inorganic N is assimilated by corn and immobilized by microbes; the N mineralization–immobilization turnover (MIT; Jansson and Persson, 1982) driven by the microbial activity (microbial succession; Beek and Frissel, 1973; Molina and Smith, 1988) shuttles N between NH_4^+ and the microbial biomass. The MIT also stabilizes some N in the SOM which decays at a lower rate than the microbial population, thus gradually reducing the rate of MIT and N accessibility to corn. Rhizodepositions recycle N in soil. They also provide the energy and C for N immobilization and microbial growth. The former process reduces N accessibility, and the latter increases it by stimulating the rates of rhizodeposition decay and MIT.

The model uses four SOM pools: two for the microbial biomass (Pool I, labile and resistant) and two more stabilized pools (Pool II and III). A very rapid rate of microbial decay was required to obtain the simulated kinetics (2 and 17 d for the half life of the labile and resistant microbial pools). These values were used throughout the simulations carried out with the models NCSWAP/NCSOIL and NCSOIL (e.g. Nicolardot et al., 1994). They are also in the order of the decay rates measured for live or dead microbes as well as microbial components added to soil (Nelson et al., 1979). It is this
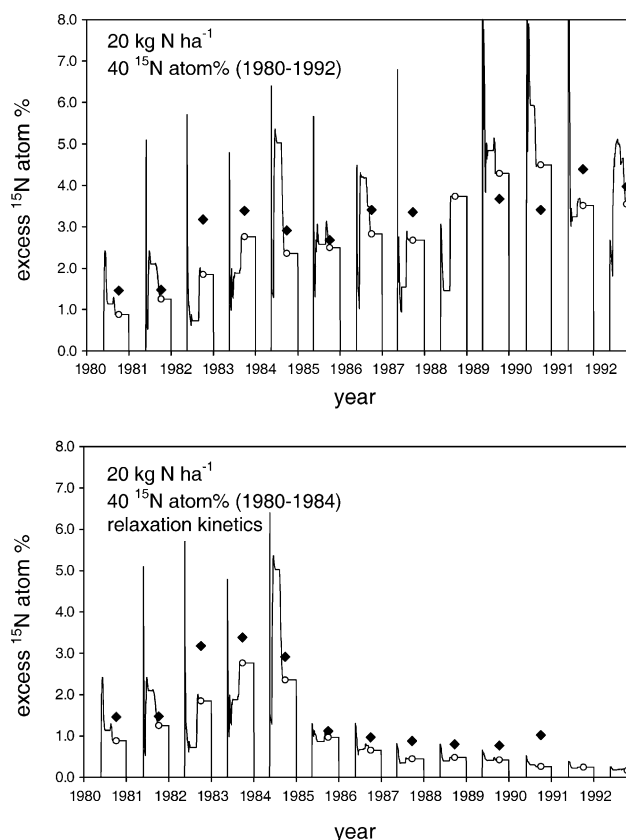

Fig. 6. Tracer ^{15}N in above-ground corn for the 20 kg N ha^{-1} with 40 ^{15}N at.%, and 2 periods of ^{15}N applications: 1980–1992 and 1980–1984: (━━━━) simulated, (○) simulated at time corresponding to measured data, (◆) measured.
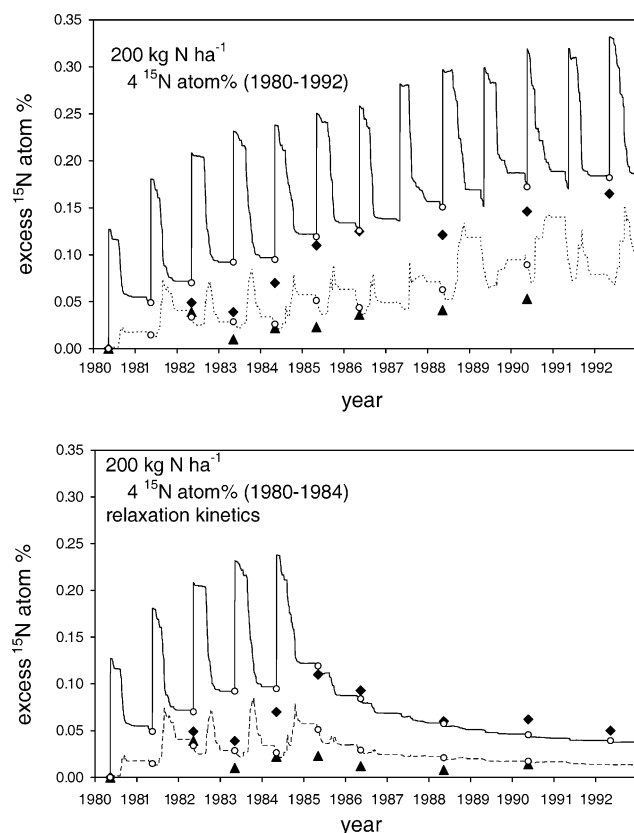
Fig. 7. Inorganic plus organic tracer ^{15}N in soil for the 200 kg N ha^{-1} with 4 ^{15}N at.%, and 2 periods of ^{15}N applications: 1980–1992 and 1980–1984: simulated (▬▬▬) 0–15 cm, (- - -) 15–30 cm; (○) simulated at time corresponding to measured data; measured (♦) 0–15 cm, (▲) 15–30 cm.

short half-life which drives the MIT at a rate fast enough to recycle 14% of the N-rhizodeposition back into the corn before it reaches maturity. The ^{15}N enrichment of the inorganic N recycled in corn was different from that of the rhizodeposition from which it was derived as it was diluted in the NH_4^+ pool during the MIT.

The simulated gross mineralization and immobilization in 1980 were 373 and 319 kg N ha^{-1} yr^{-1} in the top 0–15 cm soil layer, respectively. It corresponds to an average 1.57 and 1.35 µg N g^{-1} d^{-1}, respectively; these values are in the order of those found for a soil incubated under optimum laboratory conditions (Broadbent, 1965; Molina et al., 1990). Gross N mineralization rates ranging from 0.21 to 4.66 µg N g^{-1} d^{-1} were reported by Watkins and Barraclough (1996), and Monaghan and Barraclough (1997). For the whole profile and over one year, these rates translated to very high levels of MIT. In 1980, the simulated gross N mineralization and immobilization were 3577 and 3017 kg N ha^{-1}, respectively. It provided 559 kg mineralized $NH_4^+ - N$ ha^{-1}, a high value consistent with a soil fertility level able to sustain maximum corn yield for 4 years with only 20 kg fertilizer N ha^{-1}.

Although the same amount of ^{15}N (8.0 kg ^{15}N ha^{-1}) was added with the two levels of fertilizer N (200 and 20 kg N ha^{-1}), the different enrichments

(40 and 4 ^{15}N at.%) induced differences in the soil and plant ^{15}N enrichment. This concentration effect was caused by the obligatory passage of ^{15}N though the inorganic N pool. The intense rate of MIT which shuttled N between the organic and inorganic pools caused the adjustment of the organic ^{15}N enrichment to that of the inorganic pool fixed once a year by the fertilizer addition. Inorganic N losses by denitrification and leaching in this ^{15}N experiment were reported by Gollany et al. (2004). When corn stover was removed, the simulated denitrification losses were less and NO_3^- leaching losses were greater than when crop residue was returned. Simulated losses by both means were greater at 200 compared to 20 kg N ha^{-1} fertilization. Predicted losses of N were no more than 25% of applied N, but were somewhat larger than estimates obtained from most field observations (Gollany et al., 2004).

When ^{15}N was not added with the fertilizer N from 1985 to 1992, the sudden fall of ^{15}N enrichment in corn may have originated from a reduced N availability from soil, the fall of the SOM ^{15}N enrichment, or a combination of those factors (Figs. 5 and 6). By contrast, the soil ^{15}N enrichment decrease was more gradual, and leveled to about one-half of its peak values attained in 1984 (Figs. 7 and 8). These features could indicate that different SOM pools were exploited by the plant roots. Assuming that plant N
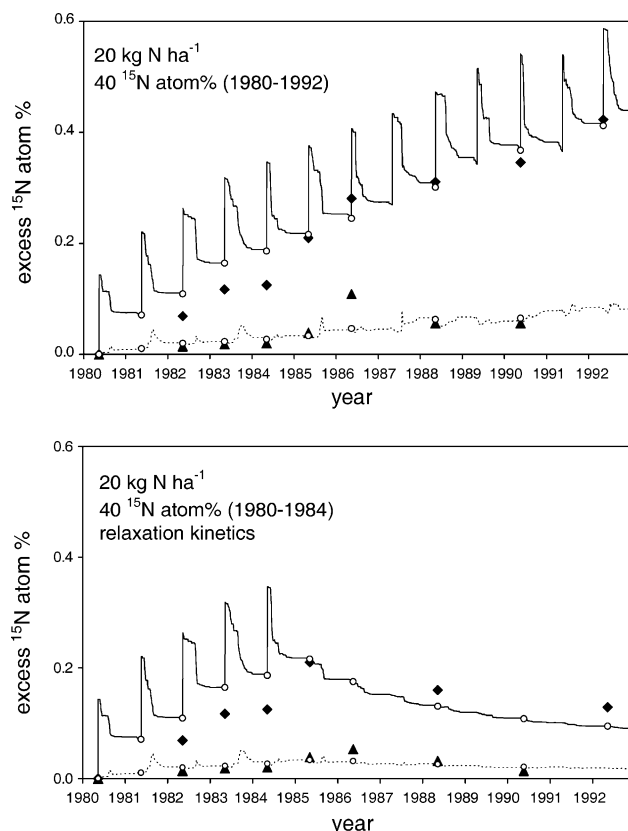

Fig. 8. Inorganic plus organic tracer ^{15}N in soil for the 20 kg N ha^{-1} with 40 ^{15}N at.%, and 2 periods of ^{15}N applications: 1980–1992 and 1980–1984: simulated (▬▬▬) 0–15 cm, (- - -) 15–30 cm; (○) simulated at time corresponding to measured data; measured (♦) 0–15 cm, (▲) 15–30 cm.
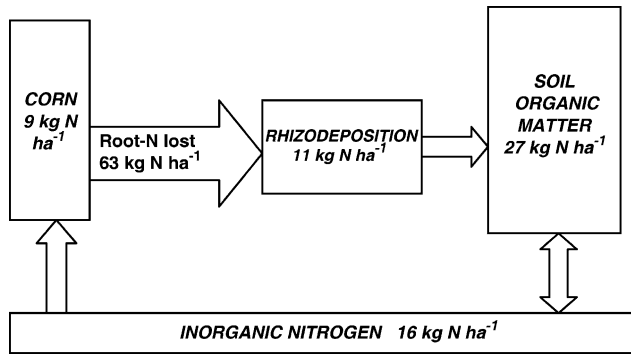
Fig. 9. Flow from emergence to maturity and accumulation at maturity of corn N rhizodeposition.

absorption was achieved through inorganic N exclusively, the change in ^{15}N enrichment in corn and soil would be controlled by the decay rates of the various SOM pools. The simulated relaxation kinetics were obtained concomitant to a gradual disappearance of ^{15}N content in Pool I and Pool II, and accumulation in the stable Pool III (Fig. 10). By 1982, Pool I and Pool II had lost almost all the added ^{15}N (0.044 and 0.162 kg ^{15}N ha^{-1}, respectively), whereas Pool III had accumulated 1.49 kg ^{15}N ha^{-1} (0.755 µg ^{15}N g^{-1} soil) in the 0–15 cm layer. By contrast, the soil pools could not be distinguished in terms of ^{15}N enrichment (Fig. 10). These
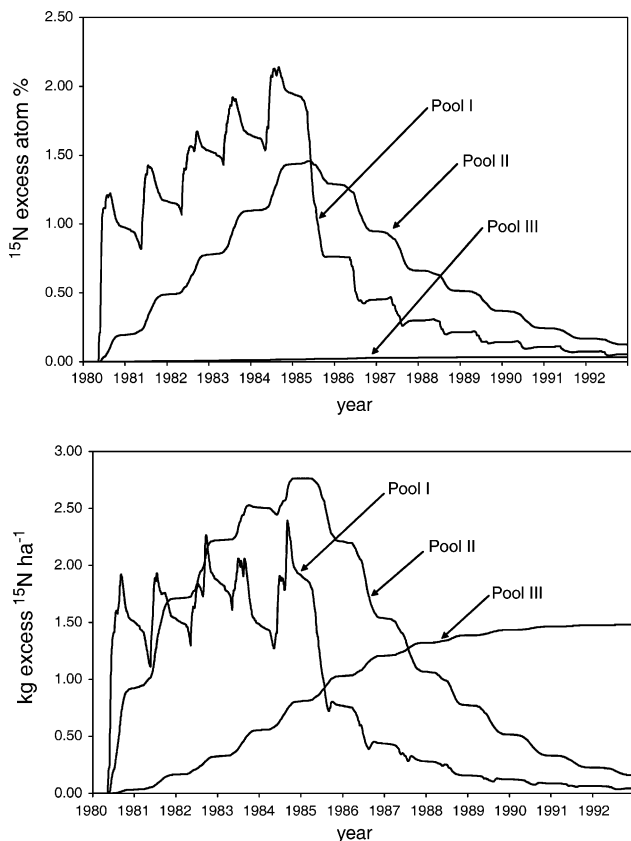
circumstances could provide a key to experimentally differentiate Pool III from the other pools: Chemical fractions from 0 to 15 cm layer of 1992 soil samples should have a low ^{15}N enrichment but high ^{15}N content to represent Pool III.

Fig. 10. ^{15}N enrichment and concentration in the SOM pools in the 0–15 cm layer, for the 200 kg N ha^{-1} treatment with ^{15}N addition discontinued in 1985.

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